In Vitro Variability Among Isolates of Eight *Phytophthora* Species in Response to Phosphorous Acid

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ABSTRACT

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The ED_{50} values for inhibition of mycelial growth in vitro by phosphorous acid (H_3PO_3) ranged from 5.2 to 224.4 μg/ml for nine *Phytophthora* species. Among the most sensitive species were *P. citricola*, *P. citrophthora*, and *P. cinnamomi*. One of the most tolerant species was *P. megasperma* f. sp. *medicaginis*. At the extreme of the range, *P. infestans* from potato had an ED_{50} value of 224.4 μg/ml. Even among a group of similarly sensitive isolates, it was possible to differentiate them at a species level in terms of their growth response to H_3PO_3. Isolates of *P. citricola* from avocado were inhibited by 48.3–67.6%, and those of the A2 mating type of *P. cinnamomi* by 11.3–38.5%, in the presence of 5 μg/ml H_3PO_3. Isolates of *P. citrophthora* from citrus were inhibited 80.3–89.3%, compared with 27.9–58.8% for isolates of *P. parasitica* in the presence of 10 μg/ml H_3PO_3.

Additional key words: Aliette, efosite-Al, fosetyl-Al, fosetyl-Na, fungicide, phosethyl-Al.

The fungicide fosetyl-Al (aluminum tris-*O*-ethyl phosphonate), which is produced as an 80% wettable powder formulation by Rhône-Poulenc Agrochimie of Lyon, France, under the trade name of Aliette®, is active against many soilborne plant diseases caused by *Phytophthora* (1,6,17,23,24). Until recently, its mode of action in vivo was thought to involve primarily an alteration in host metabolism rendering the plant less susceptible to fungal attack (2,3,9,13–15,17,20,22,24). In part, this conclusion was reached because fosetyl-Al was found to have very low activity against mycelial growth of *Phytophthora* spp. in vitro (2–4, 10,18,19,21,22,24). In one study, however, it was observed that the ED_{50} for linear mycelial growth of *Phytophthora citrophthora* (Smith & Smith) Leonian was only 56 μg/ml, although the equivalent ED_{50} for *P. parasitica* Dastur was 929 μg/ml (10). Some significant in vitro activity has been detected at different points in the life cycle of several species of *Phytophthora* (4,10,21). For instance, sporangium formation in both *P. parasitica* and *P. citrophthora* was completely inhibited by fosetyl-Al at only 10 μg/ml (10). Similarly, with *P. cactorum* (Lebert & Cohn) Schroeter and *P. citricola* Sawada, concentrations of fosetyl-Al at 10–40 μg/ml were inhibitory to the formation of both sporangia and zoospores (4).

Recently a more critical examination of the effects of fosetyl-Al on mycelial growth of several *Phytophthora* species in vitro demonstrated that the phosphate content of the medium has an effect on activity (11). On a high-phosphate medium, fosetyl-Al caused only a slight inhibition of mycelial growth of two *Phytophthora* species. However, there was strong inhibition on a medium containing a low content of phosphate with ED_{50} values for fosetyl-Al for several isolates of two *Phytophthora* species ranging from 45 to 54 μg/ml. Presumably high levels of phosphate could interfere with the uptake of fosetyl-Al by the fungus (11).

In plant tissues, fosetyl-Al is thought to degrade to phosphorous acid (H_3PO_3) (3,20,22,23). In vitro, H_3PO_3 was found to be much more active than fosetyl-Al against mycelial growth of several *Phytophthora* species and the phosphate content of the medium had little or no effect on efficacy (11). H_3PO_3 appears to be the toxophore responsible for inhibition of *Phytophthora* species when host plants are treated with fosetyl-Al (11).

The purpose of this present study was to establish the in vitro sensitivities of isolates of eight *Phytophthora* species to H_3PO_3.

MATERIALS AND METHODS

In all the in vitro tests, H_3PO_3 and fosetyl-Na (sodium ethyl phosphonate) were added to agar media before autoclaving and the pH was adjusted to 6.2 with KOH. Fosetyl-Na was used in preference to fosetyl-Al since the latter causes a precipitation of aluminum hydroxide.

The solid media employed were either a modified Ribeiro's synthetic medium (16) containing 0.084 mM (with fosetyl-Na) or 0.84 mM KH_2PO_4 (with H_3PO_3) and no β-sitosterol (11), cornmeal agar, or rye-seed medium A (5). A 0.4-cm-diameter agar disk from an actively growing colony was used as the source of inoculum. Agar plates were incubated in the dark at 24 C, except those of *P. infestans* (Montagne) de Bary, which were incubated at 21 C. Radial linear growth was determined by measuring colony diameters at two positions on the fungal colony. Treatments were carried out in triplicate, and the experiments were repeated two times. Controls consisted of the same media without H_3PO_3 or fosetyl-Na. The levels of H_3PO_3 used were determined in preliminary experiments and selected because they allowed good differentiation of the various isolates being tested.

ED_{50} values were calculated from linear regression lines obtained by plotting the percent inhibition of mycelial growth against the log concentration of H_3PO_3. The standard errors of the ED_{50} values were calculated from a linear regression analysis of the H_3PO_3 dosage against the growth inhibition. The fungal isolates were selected from the collection of *Phytophthora* at the University of California, Riverside. These isolates had never been exposed to fosetyl-Al in the field.

RESULTS

A comparison of single isolates of *Phytophthora* demonstrated that the growth responses obtained with fosetyl-Na and H_3PO_3 were almost exactly parallel, although H_3PO_3 was much more inhibitory (Table 1). Consequently, further comparisons were carried out using H_3PO_3 only.

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TABLE 1. Inhibition of radial growth of an isolate of four *Phytophthora* species on a modified Ribeiro's medium amended with either fosetyl-Na or phosphorous acid (H_3PO_3)[w]

Species	Isolate	Inhibition (%)[x] of radial growth by fosetyl-Na at (μg/ml): 80.5	241.0	482.0	ED_{50} values (μg/ml) Fosetyl-Na	H_3PO_3[y]
P. citricola	P1273	56.0 a[z]	79.4 a	92.2 a	82.0	7.0
P. cinnamomi	Pc402	24.5 b	52.7 b	76.4 b	202.8	11.9
P. capsici	P1319	23.6 b	37.5 c	62.9 c	310.5	34.7
P. parasitica	M134	21.5 b	43.0 c	59.5 c	314.1	30.9

[w] The medium at pH 6.2 contained 0.084 mM KH_2PO_4, no β-sitosterol, and the growth was measured at 4 days.
[x] Inhibition based on comparison to unamended medium.
[y] The ED_{50} values for H_3PO_3 are taken from Table 8.
[z] Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 2. In vitro responses to phosphorous acid (H_3PO_3) among isolates of *Phytophthora cinnamomi* and *P. citricola* from avocado and other hosts[x]

Phytophthora species and mating type	Isolate	Host	Inhibition (%)[y] of radial growth by H_3PO_3 at 5 μg/ml
P. citricola	P475	Avocado	67.6 a[z]
	P1287	Avocado	64.8 a
	P1273	Avocado	57.3 b
	P602	Avocado	53.8 b
	P1277	Avocado	48.3 c
P. cinnamomi A2	Pc290	*Juniperus*	44.8 c
A2	Pc352	Avocado	38.5 d
A2	Pc289	*Cedrus*	30.4 e
A1	Pc300	*Camellia*	25.4 f
A2	Pc356	Avocado	22.6 fg
A2	Pc311	Avocado	22.5 fg
A1	Pc21	*Camellia*	18.8 g
A2	Pc336	Avocado	18.8 g
A2	Pc402	Avocado	11.3 h
A1	Pc271	*Banksia*	6.3 i
A1	Pc97	*Camellia*	0.0 j
A1	Pc138	Avocado	0.0 j

[x] The medium at pH 6.2 contained 0.84 mM KH_2PO_4, no β-sitosterol, and the growth was measured at 7 days.
[y] Inhibition based on comparison to unamended medium.
[z] Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 3. In vitro responses to phosphorous acid (H_3PO_3) among isolates of *Phytophthora citrophthora* and *P. parasitica* grown on a modified Ribeiro's medium[x]

Phytophthora species	Isolate	Host	Inhibition (%)[y] of radial growth by H_3PO_3 at 10 μg/ml
P. citrophthora	M143	Citrus	89.3 a[z]
	P1163	Citrus	87.1 ab
	M132	Citrus	85.1 ab
	M117	Citrus	84.9 ab
	M142	Citrus	84.1 ab
	P776	Cacao	82.0 ab
	M131	Citrus	80.3 b
P. parasitica	T131	Citrus	58.8 c
	M114	Citrus	41.5 d
	M141	Citrus	30.8 e
	M134	Citrus	30.6 e
	M152	Citrus	27.9 e

[x] The medium at pH 6.2 contained 0.84 mM KH_2PO_4, no β-sitosterol, and the growth was measured at 7 days.
[y] Inhibition based on comparison to unamended medium.
[z] Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 4. In vitro responses to phosphorous acid (H_3PO_3) among isolates of *Phytophthora megasperma* from different hosts grown on rye-seed medium[u]

Isolate	Host	Origin	Inhibition (%)[v] of radial growth by H_3PO_3 at: 20 μg/ml	50 μg/ml
P405	Soybean	Mississippi	61.9 a[z]	82.6 a[z]
P1139	Soybean	Wisconsin	53.1 b	79.0 a
P1258	*Ficus*	New Guinea	45.0 c	53.8 b
P1057	Alfalfa	California	34.7 d	51.3 b
D1-304[w]	Douglas-fir (D1)	Oregon	26.7 e	36.7 c
D1-306[w]	Douglas-fir (D1)	Oregon	26.3 e	33.8 c
D2-C17[x]	Douglas-fir (D2)	Oregon	15.0 f	13.3 ef
AL2-508 (2A)[y]	Alfalfa (AL2)	Oregon	11.8 fg	11.8 f
P1253	Chick-pea	Australia	6.3 gh	14.8 ef
P844	Alfalfa	California	2.2 hi	23.2 d
AL2-509 (3B)[y]	Alfalfa (AL2)	Oregon	0.0 hi	0.0 g
P147	Sugar cane	Louisiana	−1.5 i	20.3 de

[u] Rye-seed medium A, pH 6.2 (5).
[v] The growth was measured at 5 days. Inhibition based on comparison to unamended medium.
[w] Douglas-fir group one isolate.
[x] Douglas-fir group two isolates.
[y] Alfalfa group two isolates according to Hansen and Hamm (13).
[z] Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 5. In vitro responses to phosphorous acid (H_3PO_3) among isolates of *Phytophthora megasperma* f. sp. *glycinea* and f. sp. *medicaginis* from alfalfa, soybean, and chick-pea[x]

Isolate	Host	Origin	Inhibition (%)[y] of radial growth by H_3PO_3 at 20 μg/ml
P1139	Soybean	Wisconsin	61.8 a[z]
P509	Soybean	Mississippi	45.9 b
P406	Soybean	Mississippi	45.3 b
P506	Soybean	Mississippi	38.5 c
P510	Soybean	Mississippi	37.2 c
P405	Soybean	Mississippi	27.9 d
P1057	Alfalfa	California	27.9 d
P1253	Chick-pea	Australia	14.9 e
1133-2	Alfalfa	California	12.1 e
P1316	Alfalfa	California	9.1 ef
1129-4	Alfalfa	California	7.1 f
P127	Alfalfa	Australia	−13.6 g

[x] Isolates were grown at 24 C on rye-seed medium A at pH 6.2 (5).
[y] Inhibition based on comparison to unamended medium.
[z] Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

The growth inhibition of 12 isolates, including six from avocado (*Persea americana* Mill.), of *P. cinnamomi* Rands A1 and A2 mating types (25) ranged from 0 to 44.8% with 5 μg/ml H_3PO_3 compared to unamended media (Table 2). Five isolates of *P. citricola* from avocado were more strongly inhibited (Table 2).

Isolates of *P. parasitica* and *P. citrophthora* from citrus were compared for mycelial growth responses to H_3PO_3. *P. citrophthora* had a narrow range of inhibition from 80.3 to 89.3%, whereas isolates of *P. parasitica* were less inhibited (27.9–58.8%) (Table 3).

A definite pattern of responses emerged among a limited number of isolates considered representative of different groups of *P. megasperma* (Drechs.) (Table 4). Two soybean isolates (*P. megasperma* Drechs. f. sp. *glycinea* Kuan & Erwin) were the most sensitive to H_3PO_3 at 20 μg/ml. The two isolates from Douglas-fir (13) responded similarly. Two isolates of *P. megasperma* Drechs. f. sp. *medicaginis* Kuan & Erwin, one from chick-pea (P1253), and the other from alfalfa (P844) also demonstrated similar tolerance to H_3PO_3 at 20 μg/ml (Table 4).

A closer examination of in vitro responses of a larger number of isolates of *P. megasperma* from soybean (f. sp. *glycinea*) and alfalfa (f. sp. *medicaginis*) revealed a tendency toward separation of the types based on their host origin (Table 5), but in some instances their responses were similar.

A limited study of isolates of *Phytophthora* spp. from cacao (*Theobroma cacao* L.) showed some differential responses. *P. palmivora* (Butler) Butler isolates were usually most sensitive to H_3PO_3, *P. capsici* (Leonian) isolates were much more tolerant, and *P. citrophthora* was intermediate in sensitivity (Table 6). There was, however, some overlap among the three species, with an isolate of *P. palmivora* (P736) responding similarly to *P. citrophthora* (Table 6).

All ten A1 isolates of *P. infestans* tested were extremely insensitive to H_3PO_3 compared to isolates of the other *Phytophthora* species tested. At least 200 μg of H_3PO_3 per milliliter was required to obtain any significant growth inhibition of *P. infestans* (Table 7).

The ED_{50} values for isolates of nine *Phytophthora* species from different hosts were calculated (Table 8) from their dosage-response curves (Fig. 1). Values for isolates grown on the synthetic medium ranged from a low of 5.2 μg/ml for an isolate of *P. citrophthora* to 91.2 μg/ml for a chick-pea isolate of *P. megasperma* f. sp. *medicaginis* (Table 8). On rye-seed medium, the ED_{50} for an isolate of *P. megasperma* f. sp. *medicaginis* (P1316) was 88.9 μg/ml, while an isolate of *P. infestans* had an ED_{50} value of 224.4 μg/ml (Table 8).

Slopes of the dosage-response curves (Fig. 1) indicate that two isolates of *P. citricola* were the most sensitive to H_3PO_3, closely followed by two isolates of *P. citrophthora* from citrus and by two isolates of *P. cinnamomi* from avocado. Among the most insensitive isolates were a *P. cactorum* isolated from *Rhaphiolepis indica*, a *P. megasperma* from chick-pea, and isolate P1257 of *P. boehmeriae*.

DISCUSSION

Fosetyl-Al has been shown to provide excellent control of a number of soilborne plant diseases caused by *Phytophthora* (1,6,23,24), because foliar applications provide systemic protection through its strong basipetal mobility (1,17,24). However, this fungicide has not controlled potato late blight caused by *P. infestans* (1,17,23).

Fosetyl-Al was believed to have little in vitro activity against *Phytophthora* because ED_{50} values frequently were found to be 500–1,000 μg/ml or even greater (2,10,17–19,23,24). Recently, much greater activity was demonstrated by using a synthetic medium that was low in phosphate (0.084 mM KH_2PO_4); ED_{50} values of 45–54 μg/ml were obtained for several isolates of two *Phytophthora* species (11). In addition, it was determined that H_3PO_3 was 6–14 times more active than fosetyl-Al in inhibiting mycelial growth.

The present study established closely parallel effects of fosetyl-Na and H_3PO_3 on mycelial growth of four isolates of *Phytophthora*. It also confirmed the greater sensitivity of *Phytophthora* spp. to H_3PO_3 compared to fosetyl-Na.

TABLE 6. In vitro responses to phosphorous acid (H_3PO_3) among isolates[x] of *Phytophthora* species from cacao

Species	Isolate	Origin	Inhibition (%)[y] of radial growth by H_3PO_3 at 10 μg/ml
P. palmivora	P922	Malaysia	81.4 a[z]
P. palmivora	P832	Trinidad	78.5 b
P. palmivora	P1020	Nigeria	73.6 c
P. citrophthora	P1213	Brazil	56.7 d
P. citrophthora	P1212	Brazil	56.1 d
P. palmivora	P736	Ghana	53.0 e
P. citrophthora	P776	Brazil	43.6 f
P. citrophthora	P1201	Brazil	40.1 g
P. capsici	P782	Cameroun	30.9 h
P. capsici	P632	Brazil	20.5 i
P. capsici	P1195	Mexico	−0.85 j

[x]Isolates were grown on Difco cornmeal agar at 24 C.
[y]The growth was measured at 4 days. Inhibition based on comparison to unamended medium.
[z]Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 7. In vitro responses to phosphorous acid (H_3PO_3) among A1 mating type isolates of *Phytophthora infestans*[x]

Isolate	Origin	Inhibition (%)[y] of radial growth by H_3PO_3 at 200 μg/ml
P1297	Ireland	71.2 a[z]
P4	Mexico	69.0 ab
P1296	Ireland	67.1 ab
P1298	Wales	63.5 abc
M3	Mexico	61.0 abc
P1293	Scotland	57.6 bc
M4	Mexico	57.1 bc
P1300	Wales	52.9 c
P1295	Scotland	40.3 d
65	Mexico	30.4 d

[x]Isolates were grown on rye-seed medium A at 21 C (5).
[y]The growth was measured at 7 days. Inhibition based on comparison to unamended medium.
[z]Means with the same letter are not significantly different ($P = 0.05$) according to Duncan's new multiple range test.

TABLE 8. ED_{50} values[a] for inhibition of radial growth expressed in micrograms per milliliter for individual isolates of nine *Phytophthora* species varying in response to phosphorous acid (H_3PO_3)

Species	Isolate	ED_{50} (μg/ml)	Standard deviation[b]
P. citrophthora	M143	5.2	± 3.7
P. citricola	P1287	6.8	± 1.1
P. citricola	P1273	7.0	± 1.7
P. cinnamomi A1	Pc97	9.0	± 0.9
P. cinnamomi A2	Pc356	9.9	± 1.6
P. citrophthora	P1163	10.4	± 2.7
P. cinnamomi A2	Pc402	11.9	± 0.7
P. capsici	P1091	18.5	± 0.9
P. megasperma f. sp. *glycinea*	P405	22.3	± 2.6
P. capsici	P1314	30.6	± 1.5
P. parasitica	M134	30.9	± 2.3
P. capsici	P1319	34.7	± 4.8
P. boehmeriae	P1257	40.6	± 8.3
P. cactorum	P1235	67.1	± 11.6
P. megasperma (chick-pea)	P1253	91.2	± 69.0
P. megasperma f. sp. *medicaginis*	P1316[c]	88.9	± 14.8
P. infestans	P1300[c]	224.4	± 10.8

[a]Isolates of *Phytophthora* grown on modified Ribeiro's medium.
[b]Mean ± standard deviation of the mean based on a linear regression of the response (percent mycelial inhibition) plotted against the dosage (log concentration H_3PO_3).
[c]These isolates were grown on cleared rye-seed medium.

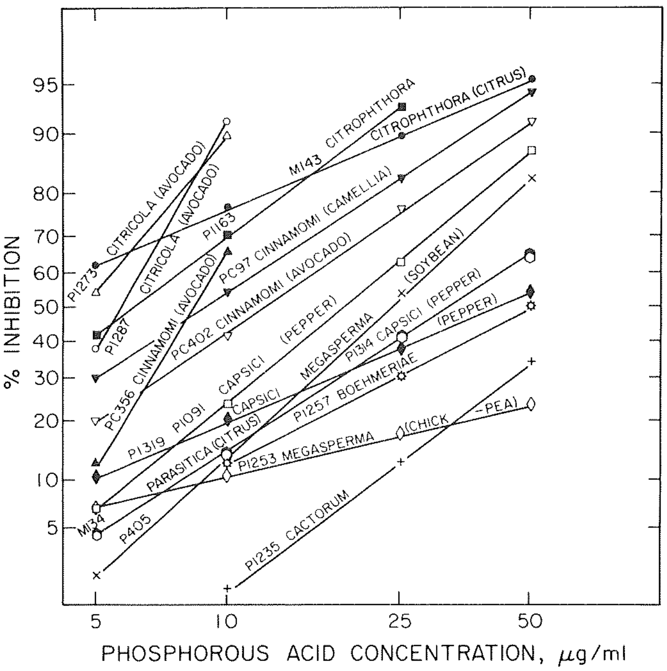

Fig. 1. Dosage-responses for 15 isolates of eight *Phytophthora* species, relating their growth response, expressed as a linear regression, to log concentration of phosphorous acid (H_3PO_3).

When groups of isolates of different *Phytophthora* species were compared, responses to H_3PO_3 in many instances were found to be characteristic for a species. For instance, all isolates of *P. citricola, P. citrophthora,* and *P. cinnamomi* were found to be extremely sensitive with ED_{50} values of 5–10 $\mu g/ml$. Despite their similar sensitivity, it was usually possible to separate *P. citricola* from *P. cinnamomi* by using a low level of H_3PO_3 (5 $\mu g/ml$).

Farih et al (10) compared single isolates of *P. citrophthora* and *P. parasitica* from citrus and obtained ED_{50} values of 56 and 929 $\mu g/ml$, respectively, for inhibition of mycelial growth by fosetyl-Al on V-8 juice agar. In the present study, several isolates of the two citrus pathogens demonstrated parallel, though more dramatic, responses to H_3PO_3 with ED_{50} values of 5–10 $\mu g/ml$ for *P. citrophthora* and about 30 $\mu g/ml$ for *P. parasitica*.

Results obtained with isolates of *P. megasperma* also produced some evidence for characteristic responses to H_3PO_3 based on formae speciales or morphological types (13). In particular, the isolates of *P. megasperma* f. sp. *medicaginis* (alfalfa host) were much less sensitive to H_3PO_3, with ED_{50} values around 90 $\mu g/ml$, compared with values around 20 $\mu g/ml$ for isolates of *P. megasperma* f. sp. *glycinea* (soybean host).

Similarly, among three species from cacao, *P. palmivora* was most sensitive, *P. citrophthora* was intermediate, and *P. capsici* was most tolerant to H_3PO_3, although there were some exceptions to this generalization. In view of the present gaps in our taxonomic knowledge of the "*P. palmivora* complex" (25), exceptions to the rule might be expected.

Metalaxyl, a fungicide that is also highly active against *Phytophthora* (17,25), also affects species differently in vitro (7). The specific mode of action of metalaxyl involves inhibition of an α-amanitin-insensitive, RNA polymerase-template complex (8). Interestingly, some of the most metalaxyl-sensitive species, such as *P. boehmeriae, P. megasperma* f. sp. *medicaginis,* and *P. parasitica* (7), were among the most tolerant to H_3PO_3. Conversely, species like *P. citrophthora* and *P. citricola*, which were relatively insensitive in vitro to metalaxyl (7), were very sensitive to H_3PO_3.

The high biological activity of H_3PO_3 against *Phytophthora* spp. indicates a specific effect of this toxophore against those pathogens. Such a concept must be reconciled with the alternative evidence that fosetyl-Al, and presumably therefore H_3PO_3, causes a stimulation of a host defense response (2,3,9,12,14,20–22). Further data will be required on the biological and chemical effect of H_3PO_3 and fosetyl-Al, in vivo and in vitro, before this question can be resolved.

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